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Mating strategies and monogamy in a territorial breeding anuran, *Rana dalmatina*: a result of sexual conflict?

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In anurans, sexual conflict of interest between the sexes over the mating system should be exacerbated by external fertilization and male-biased sex-ratio. However, the agile frog *Rana dalmatina* exhibits numerous monogamous characters despite a lack of parental care. Each caller was found to defend a distinct territory but, upon the female arrival, the frequency of calling males decreased. The number of observed amplexus and the number of clutches were strictly equal to the number of females. Examining sexual differences in the optimal mating system, sexual parasitism (4.2 %), synchronous polyandry (5.2 % of the clutches) and successive polygyny (4.2 %) were found as alternative strategies. Genetic polyandry was evidenced in 18 % of the clutches. Satellite activities are related to the increase of competitive interactions and result in a strong female harassment. Thus, sexual conflict influenced the development of alternative strategies. These results suggest that female multiple amplexus may be regarded as a forced mating strategy resulting in a coercive polyandry. In contrast, resulting both from the male territorial behavior and from the synchronous arrival of females, the prevalent monoandrous mating system should reduce the sexual antagonism.

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INTRODUCTION

In most species, males can maximize their fitness by multiplying mates with numerous partners, whereas females cannot increase their progeny by mating with many males (BATEMAN, 1948; ARNOLD & DUVALL, 1994). This reasoning led to the hypothesis that most monogamous or monoandrous breeding systems chiefly depend upon restricted access to resources or on the need for parental care, and emphasized the role of female mate choice (WITTENBERG & TILSON, 1980; CLUTTON-BROCK, 1989; REYNOLDS, 1996). Thus, mating system and pair cooperation are affected by resource dispersion in numerous socially monogamous birds (DAVIES, 1989; KEMPENAERS, 1995). Interestingly, breeding systems have proven more perplexing than previously imagined. Thus, the reasons why animals are monogamous

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are unclear when no resources are defended and no parental care occurs. Furthermore, numerous recent studies have revealed a growing evidence for multiple mating in several species formerly regarded as socially monoandrous. Polyandry is found practically ubiquitous in insects (ARNQVIST & NILSSON, 2000), but it was also inferred in reptiles (MADSEN et al., 1992), birds (BIRKHEAD & MØLLER, 1995; HASSELQUIST et al., 1996; DOUBLE & COCKBURN, 2000) and mammals (HOOGLAND, 1998; SCHENK & KOVACS, 1995; WILMER et al., 2000).

Because of their external fertilization mode and their generally weak or inconsistent parental care, multiple mating and sperm competition should be common phenomena in anuran amphibians (ROBERTS et al., 1999). The promiscuity of males chorusing in breeding congregations (HALLIDAY & TEJEDO, 1995; HÅKANSSON & LOMAN, 2004) should facilitate multiple paternities in egg masses by simple spermatic diffusion. Moreover, many anuran species exhibit a noticeable sexual size dimorphism in favor of females and a male-biased sex-ratio (GEISSELMANN et al., 1971; BLAB, 1986; READING et al., 1991; LODÉ et al., 2005), since males arrive precociously and usually stay for a longer time than females in the breeding site. Such a male-biased sex-ratio could increase competitive interactions and may result in multiple males amplecting with a single female (FUKUYAMA, 1991; JENNIONS et al., 1992; HALLIDAY & TEJEDO, 1995). Surprisingly, only few studies referred to genetic polyandry within a single clutch in the wild although multiple amplexus were commonly reported in anurans. Polyandry as a result of multiple amplexus was revealed by DNA finger printing in *Agalychnys callidryas* (D'ORGEIX & TURNER, 1995). Similarly, synchronous polyandry was inferred from protein electrophoresis in *Crinia georgiana* (ROBERTS et al., 1999) and in *Rana dalmatina* (LODÉ & LESBARRÈRES, 2004; LODÉ et al., 2004). Moreover, multiple spawning was observed in *Leptodactylus* (PRADO & HADDAD, 2003) and high multiple paternity was evidenced from egg masses in *Rana temporaria* (LAURILA & SEPPÄ, 1998). It may be alleged that polyandry provides no real advantages for most anurans showing a lack of parental care (see REYNOLDS, 1996), but the potential for multiple genetic paternity was not often investigated.

By contrast, there are some anuran species in which multiple amplexus were rarely or never observed, so that they could be regarded as socially monoandrous species. Here monoandry refers to a female mating with a single male (but a male may have several successive amplexus), whereas monogamy corresponds to a single male mating with a single female. Thus, the agile frog *Rana dalmatina* could be thought as a typically monoandrous species, as one female releases a single clutch during the breeding season and synchronous multiple amplexus has never been reported (GEISSELMANN et al., 1971; BLAB, 1986; HETTYEY et al., 2005). It is however difficult to hypothesize how monoandry could be favoured in the absence of evolutionary advantages. Most of studies on sexual selection focused on female mate choice but the evolutionary question rests in the asymmetry of interest between the sexes, i.e., the sexual conflict (RICE, 2000). Resulting from the deviation of potential fitness of males and females, sexual conflict is virtually omnipresent and stems from competition between males for the fertilization of eggs (RICE, 2000). Genetic interest of male and female do not only diverge but, in frogs, the sexual conflict should be exacerbated by the male-biased sex ratio and the external fertilization. Agile frogs do not form choruses and, as most precocious breeding anurans, do not forage during the breeding season, so that neither resource dispersion nor the need for parental care do clearly influence their reproductive behavior and monoandry. Competition within sexes mostly leads to alternative mating

Source : MNHN, Paris

strategies (TABORSKY, 1994; LUCAS & HOWARD, 1995), but the evolution of such tactics may increase the variance in reproductive success (NEFF, 2001) and therefore influence the conflict between the sexes (GAVRILETS et al., 2001; JONES et al., 2001). Consequently, it could be predicted that male and female should adopt different optimal mating strategies as a result of sexual conflict (RICE, 2000; see also LODÉ, 2006). Actually, although there is a lack of empirical studies, the sexual conflict is proved to raise an important issue in evolutionary biology (GAVRILETS et al., 2001; CHAPMAN et al., 2003), but how monogamy may reduce the sexual conflict is still hardly ever evoked.

Widely found throughout Europe, the agile frog *Rana dalmatina* is a nocturnal and terrestrial anuran which gathers in small breeding congregations during approximately 20 days from February to March. Amplexus is axillary and frog amplecting pairs are distant from each others.

By examining variations in the agile frog mating system, this paper aims at investigating whether sexual differences in optimal mating result in alternative reproductive strategies. Exploring the basis of sexual conflict, i.e., alternative strategies in male-biased frog populations, this work contributes to the understanding of the maintenance of monoandrous strategy in animals.

MATERIAL AND METHODS

MATING STRATEGIES

Field study was conducted in four breeding ponds near Redon (47°34'N, 2°50'W), western France, from 1998 to 2000. One month before the breeding period, every pond was fenced by a plastic canvas associated to buckets covered with a transparent and semi-rigid plastic. Males arrived some days earlier than females and spent more time in the pond. Captures were surveyed twice daily in order to intercept all breeding individuals. Frogs were marked (toe-clipping) and then released in the breeding pond. The breeding adult sex-ratio (ASR) was calculated as total number of males captured / total number of females captured. A quadrat with 2 m grid was set one month before in the four ponds surveyed by five observers deployed around the ponds. Frogs were located at dusk using a night optic and male locations were recorded on the quadrat map. The radius of the area of male breeding locations was estimated by measuring the distances among 72 callers. The number of caller males was estimated every night between 21 and 24 h by both auditory and visual localization by five observers, and the number of satellite males (i.e., with no calling activity) was estimated by the difference between number of callers and number of intercepted males. Samples of callers, satellites and females were hand caught, measured and immediately released. Reproductive events and aggressive behavior were monitored every night throughout the breeding season. As soon as the amplecting frogs were spawning, some animals were hand caught and measured. Every female was released after spawning. The objective of this procedure was to minimize all perturbations. The stress of frogs was considered as minimal since animals were rapidly hand caught, measured and immediately released. Every observed animal resumed normal behaviors (calling, moving or amplecting) after release.

Source : MNHN, Paris

Table 1. – Effective number of alleles (EN), observed heterozygosity (H_0) and non-biased expected heterozygosity (H_{NB}) (average ± standard deviation) in *Rana dalmatina* tadpoles collected in four ponds.

	EN	H_0	H_{NB}	*n*
Pond 1	3.33	0.4332 ± 0.061	0.5876 ± 0.056	132
Pond 2	3.33	0.3909 ± 0.120	0.5773 ± 0.072	165
Pond 3	3.33	0.4130 ± 0.125	0.5760 ± 0.065	143
Pond 4	3.33	0.4022 ± 0.099	0.5934 ± 0.083	210
Mean heterozygosity		0.4079 ± 0.094	0.5863± 0.069	650

PATERNITY ANALYSIS

Some eggs (less than 10 %) were randomly collected from 28 separated clutches to avoid diffuse fertilization and hatching tadpoles (n = 22-24 per clutch for a total of 650 tadpoles) were reared during 20 days in constant environmental conditions. Regarding ethical considerations, less than 10 % of eggs were collected to minimize the impact on frog populations as our goal was only to demonstrate multipaternity and only 22-24 tadpoles from collected clutches were instantaneously killed for genetic analysis using MS222. The others were released on the site. Paternity was inferred from allozymic data following LAURILA & SEPPÄ (1998) and ROBERTS et al. (1999). Polymorphic loci of offspring were analyzed by starch gel electrophoresis using standard techniques. Samples were homogenized in equal volume of distilled water and centrifuged at 10,000 g for 15 minutes at 4°C. Migration was performed using two buffer systems, Tris-citrate pH6 and Tris-EDTA-borate pH8. Slices were stained for revealing five specific enzymes encoded by six polymorphic loci with 2 to 5 alleles (tab. 1). From allozymic data, F-statistics were performed using Genetix software (BELKHIR et al., Genetix@crit.univ-montp2.fr) and Popgenes 32 (YEH et al., 1997). Allozyme phenotypes were considered evidences for heritable genotypes, and multipaternity was estimated using PAPA 1.0 (DUCHESNE et al., 2002). The purpose was to determine a minimal set of loci based on the expected number of parents, the possibility of sexing parents and the level of genotyping error. The parentage allocation method used in PAPA is based on the likelihood that a parental pair produces multilocus genotypes found in the tested offspring. In calculating likelihood, mating is assumed to be random and all potential parents are supposed to have equal reproductive capability. Some deviation from the latter conditions will not seriously impair the efficiency of the allocation process. Since every female produces a single clutch during the breeding season, the program PAPA simulates parental genotypes allowing estimating the minimal number of genitors for each clutch. Monoandry refers to genetic evidence of mating with a single male and polyandry with two males at least. Polygyny refers to the observation of one male fertilizing successively several clutches with no genetic evidence.

Source : MNHN, Paris

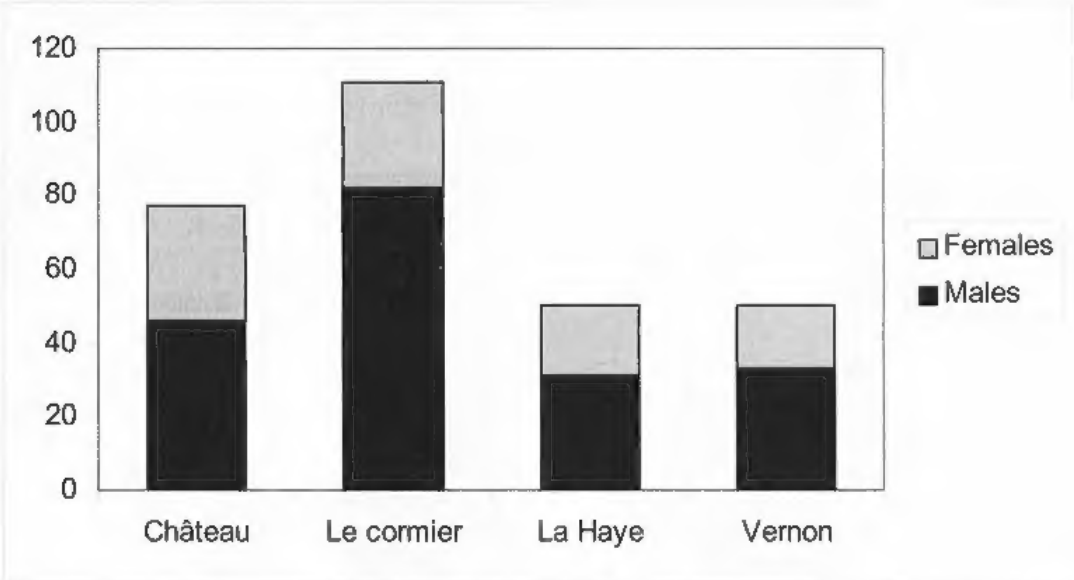

Fig. 1. – Male-biased sex-ratio in the four studied ponds as revealed by the total number of individuals intercepted.

RESULTS

MATING STRATEGIES

The adult sex-ratio was male-biased in every pond, averaging 2 males per females (SD = 0.6, ASR range 1.48-2.82, n = 288 frogs; fig. 1) with no significant differences among ponds (χ^2 = 4.75, d.f. = 3, P = 0.19). No frogs were detected in the ponds before spring dispersal, and therefore agile frogs did not hibernate under water in ponds. As soon as they arrived, most males (78.3 %, n = 92) entered the ponds and exhibited a calling activity. Each caller defended a distinct territory ranging 2.1 m in diameter (± 0.9 m, n = 72), so that callers were widely separated, and some other males arrived progressively (total males n = 192). Male intrusions into another male calling place were followed by brief chases. Females arrived with a mean of 6.5 days later than first males, but the sex-ratio remained male-biased averaging 2.0 males for a female (SD = 0.6, range 1.48-2.82, total females n = 96). With the female arrival, the frequency of calling males decreased to reach only 52.6 % (n = 192 males; fig. 2) and breeding (amplexus) extended for 9 days until the last female departure. Numerous males (47.4 %) moved around the pond side exhibiting a satellite behavior searching for mate opportunities. The mean size of callers, averaging 47.7 mm (± 5.6 mm, n = 38), was significantly higher than the size of satellites (44.1 mm ± 4.4 mm, n = 32; t = 2.97, d.f. = 68, P < 0.02).

AMPLECTING PAIRS

The number of observed amplexus and the number of clutches were strictly equal to the number of females (n = 96). Over 83.3 % of females entered water alone and went towards the

Source : MNHN, Paris

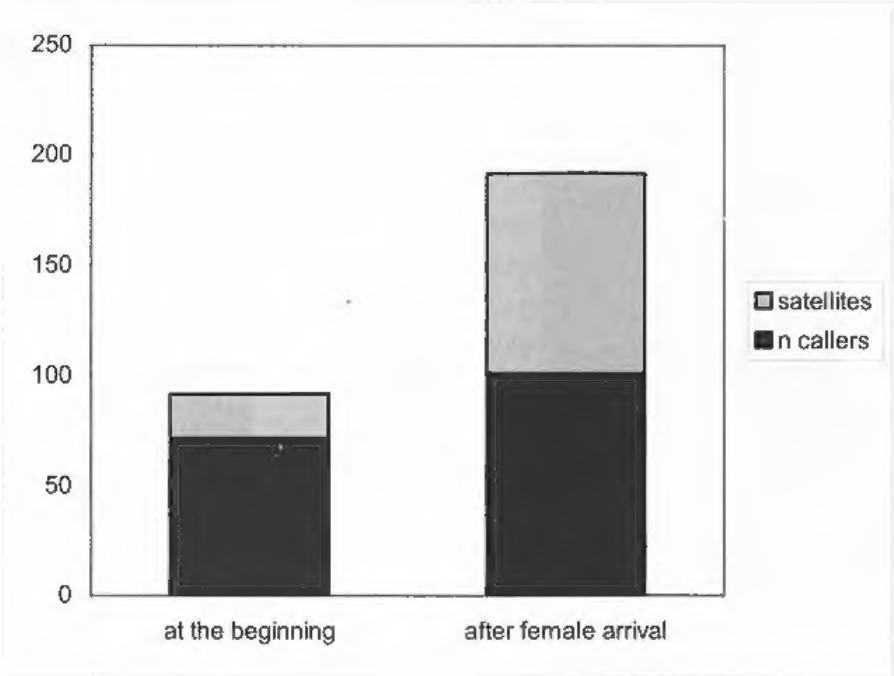

Fig. 2 – Respective number of caller and satellite males in the breeding pond at the beginning of the breeding period and after the arrival of females.

callers. However, in 16 cases (16.7 %), when a female approached the water, some male satellites tried amplecting dorso-laterally, ventrally or even over the legs of females. Hostility between sexes was evidenced since females actively rejected them. Most observed male satellites (68.8 %) gave up their amplexus attempts as soon as they intruded a caller territory or were actively rejected by the caller. After amplecting male and female left the clutch, some male satellites (4.2 %, $n = 4$ on 97) exhibited a sexual parasitism, by attempting to come above the clutch. Only five multiple amplexus on 96 (5.2 % versus 94.8% in mono-amplexus, $n = 96$) were observed for a very brief period so that the proportion of observed multiple amplexus was significantly lower than the proportions of attempts by satellites ($z = -2.544$, $P = 0.01$).

Amplecting pairs were distant from each others and females released a single clutch and then went back. The caller persisted to have a calling activity after this first amplexus during a mean of 8 days. In only four cases (4.2 %), a second female was found to consent to an amplexus with a caller which had already fertilized a clutch, realizing a successive polygyny some days after the first amplexus (mean = 3 days, range 1-5). Numerous (45 %) caller males switched for alternative behavior during the breeding period.

Paternity analysis

Five analyzed loci (*α-gdh*, *Ldh-1*, *Ldh-2*, *Mpi* and *6-Pgdh*) exhibited a pattern with at least three alleles, but enzyme *Pgm* showed a di-allelic pattern. The effective number of alleles per locus was 3.33. Among the ponds, observed heterozygosity ranged from $H_0 = 0.433$ to $H_0 =$

Source : MNHN, Paris

Table 2. – Polyandry evidences and offspring proportion resulting from a fertilization by a second male in five multiple paternal clutches as inferred from PAPA software.

	n analysed offspring	*n* estimated fathers (minimum)	Proportion of offspring corresponding to the first male	Proportion of offspring corresponding to a second male
Clutch 1	24	2	0.708	0.291
Clutch 2	24	2	0.792	0.208
Clutch 3	22	2	0.727	0.273
Clutch 4	22	2	0.818	0.182
Clutch 5	22	2	0.773	0.227
Total	114	Mean = 2	Mean = 0.763	Mean = 0.238

0.391 (tab. 2) and most loci showed significant deviation from Hardy-Weinberg equilibrium as it could be expected in samples structured into sub-samples, here clutches.

In most clutches (82.1 %, $n = 28$), paternity could be assigned to a single male per clutch using different simulations. However, for five clutches (17.9 %), a single male was unlikely to have fathered the offspring, and at least two males had shared paternity, evidencing multipaternity. In each multi-paternal clutch, a single male fertilized on average 76.2 % of the eggs whereas only 23.8 % of the eggs could be attributed to a second male, with no significant differences among clutches ($z = -1.207$, $P = 0.11$, tab. 2). No evidence for a third male fathering some tadpoles was found. Because clutches were sampled at distance from each others on different male territories, the results could not be attributable to two females. The proportion of clutches evidencing multiple paternity did not significantly differ from the proportion of satellite amplexus attempts ($z = 0.148$, $P = 0.441$) but was significantly higher than the proportion of observed multiple amplexus ($z = 2.163$, $P = 0.01$). Nonetheless, because of male pond fidelity resulted in male relatedness, multiple paternity may be higher than found. The frequency of putative successive polygyny (4.2 %) is significantly lower than the frequency of polyandry (17.9 %, $z = 2.46$, $P < 0.007$).

DISCUSSION

Sexual conflict of interest between the sexes is widely considered as an evolutionary force driving mating strategies (CARO & BATESON, 1986; GROSS, 1996; GAVRILETS, 2000; GAVRILETS et al., 2001). Indeed, interactions between sexes are recognized to influence alternative behaviors. The present study suggests that, although both synchronous polyandry and successive polygyny occurred in *Rana dalmatina*, the mating system is basically dominated by monogamous reproductive strategies, reducing sexual conflict.

Source : MNHN, Paris

ALTERNATIVE STRATEGIES

In the agile frog, whereas large males (callers) defend territories based on call advertisement, other males (satellites) actively move searching for mate opportunities. Since the discovery of sexual parasitism in the tree frog (PERRILL et al., 1978), callers and alternatively satellites have often been identified in breeding anurans (HOWARD, 1984; ARAK, 1988). Male strategies can vary throughout the lifetime. Mature dominant frogs can use durable calling activities, whereas young and subordinate animals should only adopt a search for mate behavior (LOMAN & MADSEN, 1986; HOUSTON & MCMAMARA, 1987; LUCAS & HOWARD, 1995). Agile frogs do not hibernate under water in ponds before their breeding dispersal and males have to control a call area in the spawning pond. Because the cost of defending a territory depends upon the level of competition, mature males may switch for alternative behaviors if the sex-ratio is strongly male-biased. Male-biased sex-ratio was often evidenced in anuran populations (GEISSELMANN et al., 1971; READING et al., 1991; LODÉ et al., 2005) but was rarely documented in agile frogs (BLAB, 1986). In agile frogs, callers are significantly larger than satellites but have to actively defend their exclusive breeding territory each time a satellite intrudes. Although callers show a better mating success (LESBARRÈRES et al., 2008), call advertisement constitutes a strong attractive cue for females but the call activity remains insufficient to exclude all satellites (LESBARRÈRES & LODÉ, 2002). Satellites move around the pond searching for mate opportunity and try to catch any female approaching the water. Nonetheless, most satellites do not keep the benefit of this effort and have to renounce or are evicted by the caller as soon as the female arrives in a caller territory. In most cases, satellites fail amplecting but they may marginally succeed if the caller is not vindictive enough. As it was observed in other anuran species (ROBERTS et al., 1999), such amplexus are rarely dorsal but lateral or even ventral and therefore can only lead to a partial fertilization. Thus the satellite strategy allows certain males to partly fertilize a clutch realizing a genetic polyandry. Satellite activities should be related to the increase of competitive interactions and mainly result from mating rivalry in which males compete over access to females, some males switching to alternative behavior as soon as the first females arrive. Therefore, multiple amplexus may be regarded as a forced mating strategy resulting in a coercitive polyandry. Moreover, such simultaneous polyandrous mating do not seem to allow a better fertilization as BYRNE & ROBERTS (1999) demonstrated in *Crinia georgiana*. Nevertheless, polyandry may be also thought of as a result of a secondary fertilization. Some satellite males show a sexual parasitism trying to fertilize the clutch of another pair. JENNIONS & PASSEMORE (1993) demonstrated the capability of sperm release by a second male in *Chiromantis*. Although in *Rana dalmatina* male territorial behavior perseveres and leads to a guarding behavior, such a secondary fertilization may explain the apparent discrepancy between the apparent number of multiple amplexus and the frequency of multiple paternity. Actually, multiple paternity should be underestimated in agile frogs both because allozymic variations are not the best genetic marker for polyandry and because of the breeding site fidelity of most anurans (see READING et al., 1991). Breeding site fidelity should result in increasing relatedness of breeding adults.

Anyway, whether multiple mating results from forced mating or secondary fertilization, the polyandry should restrict the evolutionary influence of female mate choice and reduce the opportunity for sexual selection (see JONES et al., 2001). However, the females actively move

Source : MNHN, Paris

towards a caller territory. Although females go to breeding territories where no female laid a clutch, alternatively some females may have amplexus with a polygynous male. Such polygyny consists in a successive polygyny since these females release their clutch in the same territory where a male fertilized a first clutch a few days ago. The reason why those females appeared to avoid mating with a previously mated male is not clear. In numerous fish species, females are more attracted by a male which guarded a clutch (BISAZZA & MARRCONATO, 1988; WARNER et al., 1991). But, in the agile frog, polygyny occurs marginally and may be interpreted as a prudent strategy performed by an inexperienced female by copying the behavior of an experienced female (SIROT, 2001). Anyway, the relative synchrony of spawning events restricts their opportunity to mate with a previously mated male. Moreover, the rareness of this strategy suggests that it is little efficient for improving the fitness. Females may restrain their polygyny to avoid the competition risk unfavorable to the tadpoles of the second clutch. Negative competitive interactions in tadpoles were widely reported (WILBUR, 1982, TRAVIS, 1984, GRIFFITHS, 1991; FARAGHER & JALGER, 1998, BARNETT & RICHARDSON, 2002). Moreover, hatched after the first, these tadpoles may suffer cannibalism from tadpoles of the first clutch (CRUMP, 1983).

THE RESULTING MATING SYSTEM

Although multiple paternity was found in at least four distinct anuran species (D'ORGEIX & TURNER, 1995, LAURILA & SEPPÄ, 1998; ROBERTS et al., 1999; LODÉ & LESBARRÈRES, 2004), their mating behavior greatly differed. The territorial defense of an exclusive individual breeding site promoted the prevalent monoandrous character of the agile frog. Indeed, both polyandry and polygyny were found to be marginal strategies and agile frogs exhibited numerous monogamous characters. As illustrated by numerous bird species (DAVIES, 1989, SANDELL, 1998), it has been proposed that female competition was the key factor for the evolution of monogamy (the female aggression hypothesis, WITTENBERG & TILSON, 1980). Nonetheless, antagonistic interactions hardly ever occurred in monogamous females and seemed unlikely to produce the frog monogamy. Mainly based on mammals, it has been also argued that monogamy evolves due to the need for parental care (CLUTTON-BROCK, 1989). Association between males and females may provide both a best feeding and safety to the progeny. Nevertheless, that monogamy was promoted by parental care was rarely supported by investigations on mating systems and was only found as special cases (KOMERS & BROTHERTON, 1997). The level of sociality of mammal females is the main parameter which influenced the male capability to control them (EMLEN & ORING, 1977, BROTHERTON et al., 1997), and KOMERS & BROTHERTON (1997) proposed that monogamy in mammals is basically due to their solitary habits rather than the need for parental care. Relating monoandry to female arrivals and dispersion of breeding males, our results suggest that monoandry in anuran is chiefly associated with the territorial breeding behavior of males and with the relative synchrony of females arrivals. Using small exclusive breeding territory, the male behavior followed the prediction that sexual territory should be small enough to allow males to defend them.

Actually, any deviation from monogamy results in an increase of sexual conflict, since in a monogamous mating system any trait that enhances the fitness of one sex also improves the fitness of the other. The main advantage of monogamy is that both male and female produce

Source : MNHN, Paris

most offspring whereas polygyny results in better success only in some males. Whereas sexual differences in mating may result in alternative reproductive strategies, the optimal response of agile frogs to the sexual conflict converges towards a monogamous breeding system achieving a sexual equilibrium. Resulting both from the male territorial behavior and from the synchronous arrival of females, the prevalent monogamous mating system reduces the sexual conflict. The reason why frogs adopt a monogamous mating system may be related to the fact that monogamy yields genetic benefits.

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A new species of the genus *Quasipaa* (Anura, Ranidae, Dicroglossinae) from northern Vietnam

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A new species of the genus *Quasipaa* from northern Vietnam is described and compared with four related species from China: *Quasipaa spinosa*, *Q. jiulongensis*, *Q. exilispinosa* and *Q. courtoisi*, the latter being here confirmed, on morphometric grounds, as a distinct species. *Q. courtoisi* differs from the four other species by measurements concerning the hands, feet and head. The new species is further distinguished from *Q. exilispinosa* by its larger webbing. It is a sibling species of *Q. spinosa* from which it differs by a higher number of nuptial spines on the prepollex and finger I of breading males.

Introduction

During his travels of exploration of the Chinese Empire, the father Armand David discovered a large frog living in torrents of the mountains in the surroundings of Jinjiang (Jiangxi Sheng), the breeding males of which emit a strong and loud call and have the chest and fingers covered with black horny spines. He described it as new on two occasions, first (David, 1872: 76) as *Rana latrans*, a nomen which later proved invalid, being a junior primary homonym, and later (David, 1875: 253) as *Rana spinosa*. This species is still known under the latter specific nomen, but it is now referred to the genus *Quasipaa* Dubois, 1992 (Ranidae, Dicroglossinae, Paini; see Jiang et al., 2005; Ohler & Dubois, 2006, Frost et al., 2006; Chi et al., 2009).

Although many nomina have been proposed in the literature for species of the genus *Quasipaa*, Ohler & Dubois (2006) only recognized 11 valid species in this genus. Among these, two informal groups can be distinguished by the aspect of their warts on the mid-dorsal skin: a group of seven species with longitudinally elongate, regularly arranged warts, some of which are quite wide and prominent, and a group of four species with smaller warts, not very prominent, rounded or slightly elongate, or if elongate not wide and regularly arranged on

Source : MNHN, Paris

back. The latter group can be provisionally designated as "*Quasipaa* sensu stricto", as it includes *Rana spinosa*, the type-species of *Quasipaa*, whereas for the former group the generic nomen *Eripaa* Dubois, 1992 (type-species *Rana fasciculispina* Inger, 1970) would be available if it proved holophyletic and had to be recognized formally as a subgenus. The four species of "*Quasipaa* sensu stricto" recognized by Ohler & Dubois (2006) include three species recognized by all recent authors (e.g., Fei, 1999; Fei et al., 2006; Che et al., 2009), i.e., *Quasipaa exilispinosa* (Liu & Hu, 1975), *Quasipaa jiulongensis* (Huang & Liu, 1985) and *Quasipaa spinosa* (David, 1875), and a species, *Quasipaa courtoisi* (Angel, 1922), usually considered as a synonym of the latter. Recent molecular data (Che et al., 2009) suggest that additional species probably require recognition in this group.

Most species of *Quasipaa* are endemic to China, but a few of them occur in the eastern part of the Indochinese peninsula (Cambodia, Laos, Thailand and Vietnam). One of them was reported under the nomen *Rana spinosa spinosa* by Bourret (1937, 1942) on the basis of 14 adult specimens collected by him on the Mau Son (then spelt Mao-Son) in northern Vietnam. Six of these specimens (5 males, 1 female) are still kept in the collections of the Paris Museum under the numbers MNHN 1938 0001-0006. A seventh specimen from the same series was transferred to the Edward H. Taylor collection and later to the Field Museum in Chicago, where it is still kept under the number FMNH 123883 (Alan Resetar, personal communication). Two additional specimens of the same species from Mau Son are known to exist in collections. The first additional one was collected in 1903 by H. Fruhstorfer between 915 and 1220 m (3000-4000 ft) in the Mau Son, along with several other frog species (Boulenger, 1903; Bourret, 1942: 13). It was identified as *Rana spinosa* by Boulenger (1920: 75). It is still kept in the Natural History Museum collection in London under the number BMNH 1903.7.2.26. Finally, a second additional specimen was part of the collection of herpetological specimens made by J. Delacour and W. P. Lowe in Tonkin and Annam in 1926 and 1927: this specimen, stated to be from Lang Son, is also probably from Mau Son (Bourret, 1942: 291). It was identified by H. W. Parker as *Rana duboisreymondi* and reported under this nomen by Angel (1928). It is still present in the Paris Museum collection under the number MNHN 1928.0025.

Although by their overall aspect these Mau Son specimens indeed resemble Chinese specimens of *Quasipaa spinosa*, they differ from them in a few respects, as discussed below. We used morphometric data to compare them with numerous Chinese specimens referred to the four species of "*Quasipaa* sensu stricto". This analysis revealed constant and significant differences between the Vietnamese specimens and all Chinese specimens, and we consider that they demonstrate the existence of a distinct species in Vietnam, which is described and named here.

Material and methods

Appendix 1 provides a list of the specimens of "*Quasipaa* sensu stricto" examined and measured for this study, along with the abbreviations used to designate the collections where they are kept. Specimens were sexed using their external characters (in the case of adult breeding males) or through a slight lateral incision in order to see one of the gonad. All

Source : MNHN, Paris

specimens examined in this study were adult, according to the criteria of DUBOIS (1976: 31-33).

Appendix 2 provides a list and descriptions of the measurements taken on these specimens. Measurements were obtained with a slide calliper to the nearest 0.1 mm, or, for values below 5 mm, with an ocular micrometer to the nearest 0.01 mm. For univariate comparisons between samples, all measurements except snout-vent length (SVL) were transformed in ratio to SVL, expressed in per thousands (‰). Subgroups were composed according to two possible criteria: taxonomic allocation and sex.

Univariate morphometric comparisons between samples were made using the non-parametric Mann-Whitney *U* test (ZAR, 1984). Multivariate factor analyses were performed using the Principal Component Analysis (PCA) with varimax rotation as implemented in the software SPSS (ANONYMOUS, 1999. 426). According to the Kaiser criterion, eigenfactors larger than 1 where retained (NORUSIS, 1992) Factors of PCA were plotted as scatterplots indicating species allocation. To examine effects of species delimitation on the principal component scores, factorial ANOVA were performed Calculations and statistical analyses were realised using SPSS statistical software (NORUSIS, 1992)

The holophoront (holotype) of the new species was described in detail using the same format and methodology as in several of our previous works on Asian anurans, in particular ranids (OHLER & DUBOIS, 1999; DUBOIS & OHLER, 2000, 2001, 2005; DUBOIS et al., 2001, VEITH et al , 2001; OHLER et al., 2002) Some of the terms used below (holophoront, hypodigm, onymotope) were defined elsewhere, and reasons were provided for using them (DUBOIS, 2000, 2005). The traditional terms of equivalent meaning are indicated below on first use between parentheses.

TAXONOMY

Quasipaa acanthophora sp. nov
(fig. 1)

Etymology of specific nomen. From the Greek ακανθος, "spine" and φερω , "I bear" This nomen is the Greek equivalent of *spinosa* in Latin.

Holophoront (holotype) MNHN 1938.0001 (ex LZUH Z.108), adult male, SVL 101 7 mm.

Onymotope (type locality) – Mau Son (21°51'N, 106°58'E), Lang Son province, Vietnam.

Other specimens of the hypodigm (paratypes). MNHN 1938.0002 (ex LZUH Z 107), 1938 0003 (ex LZUH Z.106), 1938 0004 (ex LZUH Z.115) and 1938.0006 (ex LZUH Z 109), and FMNH 123883 (ex LZUH Z.112), 5 ♂, SVL 83.0-99 5 mm; and MNHN 1938 0005 (ex LZUH Z.113), 1 ♀, SVL 81.0 mm; all collected by René Bourret in the same locality as the holophoront. MNHN 1928.0025, 1 ♂, SVL 79 0 mm, collected in 1926 or 1927 by Jean Delacour and Willoughby Prescott Lowe in the same region. BMNH 1903.7.2.26, 1 young ♂, SVL 61.3 mm, collected in 1903 by Hans Frühstorfer on the same mountain. Seven additional

Source : MNHN, Paris

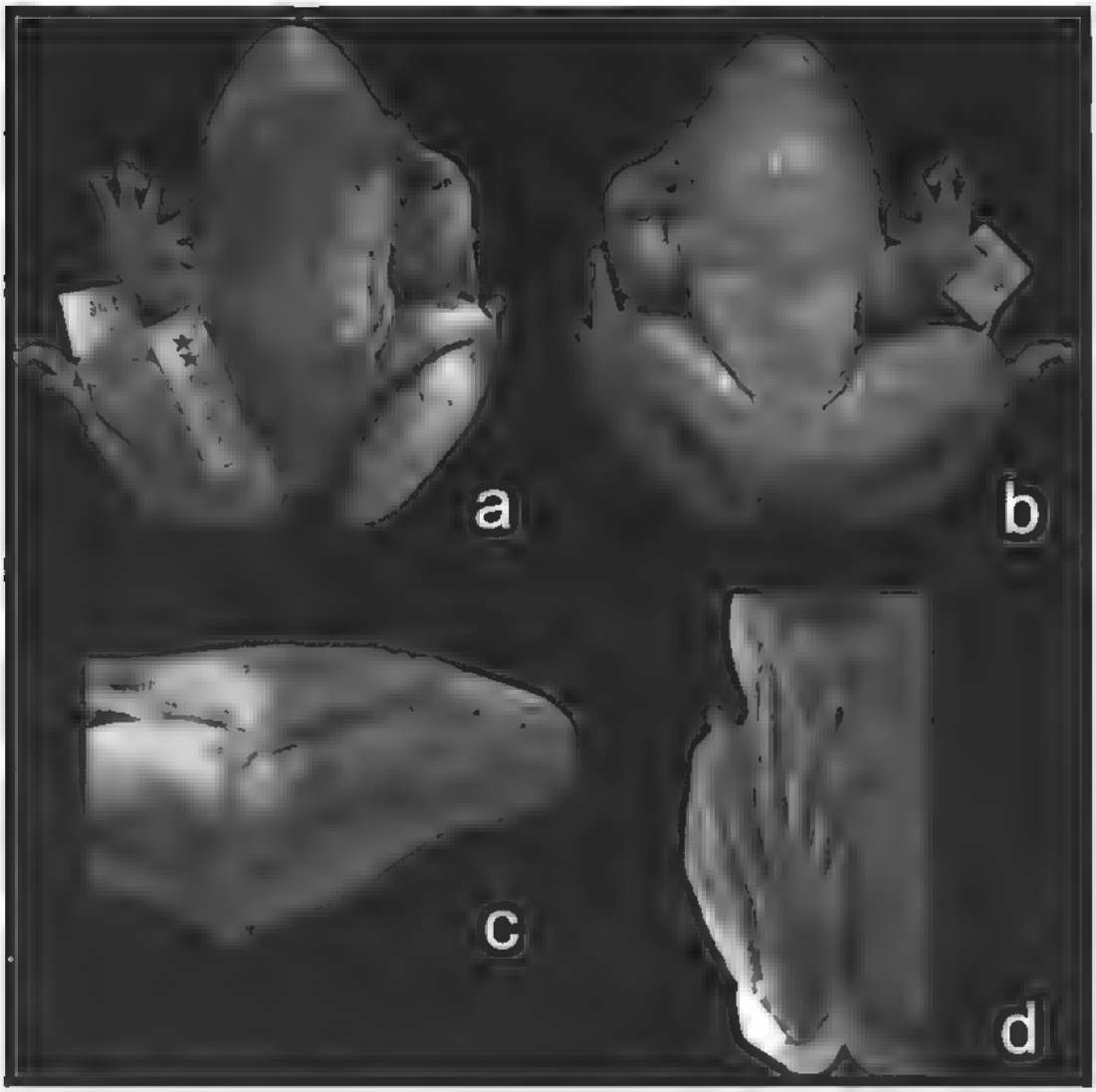

Fig. 1. *Quasipaa acanthophora* sp. nov., holophoront MNHN 1938.0001, adult male, SVL 101.7 mm. (a) Dorsal view, (b) ventral view; (c) right lateral view of head; (d) ventral view of right foot.

specimens (LZUH B 103-105, B.107, Z.110-111, Z.116) were reported by Bourret (1942: 26) from the same locality and probably belonged in the same species. We have been unable until now to locate any of them in current collections, but some might be rediscovered in the future. However, because we have been unable to examine them, we refrain to formally designate them as paratypes of the new species.

Description of the holophoront. – (A) Size and general aspect. – (1) Specimen of large size (SVL 101.7 mm), body rather stout.

(B) Head. – (2) Head rather large, wider (HW 41.0 mm) than long (HL 38.5 mm; MN 32.2 mm; MFE 25.1 mm, MBE 17.2 mm), flat above. (3) Snout rounded, slightly protruding,

Source : MNHN, Paris

its length (SL 14.4 mm) longer than horizontal diameter of eye (EL 11.2 mm). (4) Canthus rostralis indistinct, loreal region concave, flared in cross section (5) Interorbital space flat, smaller (IUE 8.1 mm) than upper eyelid (UEW 9.0 mm) and internarial distance (IN 10 0 mm); distance between front of eyes (IFE 15.3 mm) about three fifth of distance between back of eyes (IBE 26 8 mm). (6) Nostrils oval, with flap of skin laterally, closer to eye (EN 6 8 mm) than to tip of snout (NS 7.8 mm). (7) Pupil indistinct (8) Tympanum indistinct (9) Pineal ocellus present, between anterior borders of eyes. (10) Vomerine ridges present, bearing numerous small teeth (n = 10), between choanae, with an angle of 60° relative to body axis, as close to choanae as to each other, longer than distance between them. (11) Tongue large, cordate, emarginated, median lingual process absent; tooth like projection on maxilla absent.

(C) Forelimbs. (12) Arm rather short (FLL 25.9 mm), strong, shorter than hand (HAL 25.2 mm), distinctly enlarged. (13) Finger I rather long and strong; finger II rather short, rather strong; finger III rather long and strong (TFL 12 8 mm); finger IV short, relatively thin. (14) Relative length of fingers, shortest to longest: II < I < IV < III (15) Tips of fingers rounded, slightly enlarged, without discs. (16) Fingers II and III with dermal fringes; webbing absent (17) Subarticular tubercles prominent, rounded, single, all present. (18) Prepollex oval, prominent, two oval, distinct palmar tubercles; supernumerary tubercles absent.

(D) Hindlimbs. – (19) Shank three times longer (TL 53 5 mm) than wide (TW 18 8 mm), about as long as thigh (FL 52.8 mm) and distance from base of internal metatarsal tubercle to tip of toe IV (FOL 52 2 mm). (20) Toes rather short and thin; toe IV (FTL 28.9 mm) more than one third of distance from base of tarsus to tip of toe IV (TFOL 72.1 mm). (21) Relative length of toes, shortest to longest: I < II < V < III < IV. (22) Tips of toes rounded, distinctly enlarged, without discs. (23) Webbing complete: I 0 – 0 II 0 – 0 III 0 0 IV 0 0 V (WTF 16.1 mm; WFF 14.5 mm, WI 14.4 mm, WII 11 6 mm). (24) Dermal fringe along toe V well developed, from tip of toe to basis of metatarsus. (25) Subarticular tubercles very prominent, oval, simple, all present (26) Inner metatarsal tubercle long, prominent; its length (IMT 8 3 mm) 1 7 times in length of toe I (ITL 14.2 mm). (27) Tarsal ridge present, two thirds of distal parts of tarsus. (28) Outer metatarsal tubercle, supernumerary tubercles and tarsal tubercle absent

(E) Skin (29) Dorsal and lateral parts of head and dorsal part of back shagreened with regularly disposed glandular warts on back; upper part of flanks shagreened with elongated glandular warts, lower part of flanks with foldings. (30) Dorsolateral folds absent; lateral line system absent; "fejervaryan line" absent; supratympanic fold prominent, from eye to above arm; cephalic ridges absent; co-ossified skin absent. (31) Dorsal parts of limbs: forelimbs shagreened; thigh shagreened with thin foldings, legs shagreened with thin foldings and horny spinules; tarsus smooth. (32) Ventral parts of head, chest and Limbs smooth; belly with transversal foldings. (33) No macroglands.

(F) Coloration in alcohol. – (34) Dorsal and lateral parts of head and body: dorsum brown with dark brown spots around the warts; a dark brown band across upper eyelids and head; upper part of snout clearer, light brown; upper part of flank like back; lower part of flank brown with light marbling; loreal region light brown with dark brown bands, tympanic region light brown with a dark brown band underlining tympanic fold, upper lip light brown with three distinct vertical dark brown bars. (35) Dorsal parts of limbs: forelimbs, dorsal part of thigh, leg and foot brown with indistinct darker bands; posterior part of thigh dark brown

Source : MNHN, Paris

Table 1. – Maximum numbers of nuptial spines in breeding males of *Quasipaa courtoisi*, *Q. exilispinosa*, *Q. jiulongensis*, *Q. spinosa* and *Q. acanthophora*. The table gives the total number of spines on breast and the maximum numbers of spines observed on one arm (either left or right) in a given place (ppxmax, prepollex, imax, finger I, iimax, finger II, iiimax, finger III). Number of specimens observed is given in brackets. For *Q. spinosa* only males of size interval corresponding to adult size in *Q. acanthophora* were included in the analysis. The Mann-Whitney *U* test compares the spine numbers of *Q. spinosa* and *Q. acanthophora*. Significance level ***, $P < 0.001$, **, $P < 0.01$

Spine number	*Q. courtoisi*	*Q. exilispinosa*	*Q. jiulongensis*	*Q. spinosa*	*Q. acanthophora*	Mann-Whitney *U*-test
breast	153.3 ± 37.2 (7) 87-195	81.6 ± 60.7 (12) 0-198	106.9 ± 63.2 (27) 0-288	130.8 ± 27.0 (14) 88-171	139.5 ± 145.9 (6) 0-322	*U* = 39 *P* = 0.841 n.s.
ppxmax	17.7 ± 10.8 (6) 7-38	9.4 ± 5.2 (12) 2-17	11.3 ± 10.7 (27) 2-56	13.8 ± 5.6 (14) 2-22	30.5 ± 14.1 (6) 19-55	*U* = 7 *P* = 0.002 **
imax	159 (1)	28 ± 9.3 (12) 13-42	39.9 ± 21.5 (27) 22-128	67.9 ± 15.0 (14) 48-91	115.2 ± 23.8 (6) 96-162	*U* = 0 *P* = 0.000 ***
iimax	27.6 ± 15.3 (5) 0-51	9[illegible] ± 6.3 (12) 0-19	15.9 ± 8.2 (27) 4-45	23.4 ± 6.7 (14) 13-34	35.8 ± 15.6 (6) 23-59	*U* = 19.5 *P* = 0.062 n.s.
iiimax	11.3 ± 10.4 (4) 3-26	1.7 ± 2.5 (12) 0-7	4 ± 4.6 (27) 0-14	7.9 ± 5.7 (14) 1-17	15.5 ± 15.6 (6) 4-38	*U* = 32.5 *P* = 0.444 n.s.

Table 2. – Snout-vent length and ratio of SVL to body measurements for adult males and female of *Quasipaa acanthophora*

Measurements	Males *n* = 6	Female *n* = 1	Measurements	Males *n* = 6	Female *n* = 1	Measurements	Males *n* = 6	Female *n* = 1
SVL	92.1 ± 9.18 79-101.7	81.0	IN/SVL	96 ± 1.88 94-98	94	FTL/SVL	288 ± 10.27 274-302	288
HW/SVL	410 ± 31.25 398-430	395	EN/SVL	60 ± 4.7 53-67	60	IMT/SVL	83 ± 3.64 77-87	77
HL/SVL	382 ± 3.18 379-387	383	EL/SVL	115 ± 4.77 108-119	112	ITL/SVL	136 ± 7.75 121-141	144
MN/SVL	320 ± 8.76 309-334	321	FLL/SVL	252 ± 17.66 230-273	256	WTF/SVL	162 ± 5.93 157-172	159
MFE/SVL	263 ± 12.86 247-280	259	HAL/SVL	238 ± 10.4 220-248	242	WFF/SVL	143 ± 6.5 134-151	144
MBE/SVL	165 ± 10.66 144-175	170	TFL/SVL	125 ± 2.77 120-128	127	WI/SVL	148 ± 5.68 142-157	152
IFE/SVL	153 ± 7.24 141-163	148	TL/SVL	531 ± 14.07 513-554	543	WII/SVL	117 ± 7.5 106-129	127
IBE/SVL	268 ± 11.13 255-288	257	FOL/SVL	523 ± 17.29 503-541	535			

with light brown flecks. (36) Ventral parts: throat and chest brown with whitish marblings; margin of throat whitish with brown spots; belly dirty whitish; thigh dirty white with brown marbling on sides; webbing brown.

(G) Male secondary sex characters. - (37) Large-sized, black nuptial spines present on prepollex and finger I (two separate pads), fingers II and III and chest. Table 1 gives the numbers of spines in these places on both hands. (38) Forearms enlarged. (39) Vocal sacs indistinct on throat; pair, rounded openings posterior on mouth floor.

Variation – The other members of the hypodigm are similar to the holophoront in most respects. Variation concerning morphometric measurements is summarized in table 2. The dorsal colour of specimen MNHN 1938.0002 is different as this specimen is not more or less uniformly dark brown with indistinct darker spots near warts, but lighter brown with distinct dark brown patches including a band between the eyes. Six out of seven specimens show elongate fine warts either on lateral part of back or all over back.

Source : MNHN, Paris

Table 3 Principal component analysis using marivax rotation with Kaiser normalization of factor loadings for adult males of *Quasipaa courtoisi*, *Q. exilispinosa*, *Q. jiulongensis*, *Q. spinosa* and *Q. acanthophora*

A Total variance explained

PC	Initial eigenvalues			Rotation sums of squared loadings		
	Total	% of variance	Cumulative %	Total	% of variance	Cumulative %
1	7.908	34.382	34.382	5.609	24.388	24.388
2	4.262	18.531	52.913	5.090	22.131	46.519
3	2.651	11.524	64.437	3.513	15.273	61.792
4	1.713	7.448	71.885	2.063	8.968	70.760
5	1.041	4.527	76.412	1.300	5.652	76.412

B Rotated component matrix

	Component						Component				
	1	2	3	4	5		1	2	3	4	5
SVL	-0.676	-0.151	0.294	-0.506	0.163	SVL	-0.676	-0.151	0.294	-0.506	0.163
RHW	0.063	0.790	-0.077	-0.289	0.319	RIN	0.428	-0.152	0.271	0.711	-0.058
RHL	0.404	0.804	-0.025	0.236	0.054	REN	-0.045	0.362	0.012	0.057	0.754
RTL	0.729	0.233	0.046	0.215	0.091	RFL	0.507	0.569	-0.185	0.244	-0.184
RMN	0.300	0.893	-0.035	0.193	0.106	RTFL	0.747	0.177	0.219	0.117	-0.083
RMFE	0.260	0.891	-0.080	0.100	-0.040	RFTL	0.878	0.191	0.152	-0.006	-0.087
RMBL	-0.137	0.906	-0.025	-0.115	-0.070	RIMT	-0.105	-0.296	0.280	-0.100	0.648
RIFE	0.227	0.532	0.258	-0.037	-0.095	RITL	0.802	0.040	0.220	-0.030	-0.116
RIBL	0.498	0.517	-0.078	0.381	0.087	RWTF	0.142	0.088	0.876	0.076	-0.045
RFLL	0.143	-0.122	-0.217	-0.846	-0.018	RWFF	0.215	-0.220	0.860	-0.007	0.113
RHAL	0.765	0.254	0.055	-0.095	0.052	RWI	0.093	0.068	0.831	0.297	-0.020
RFOL	0.927	0.050	0.191	-0.000	0.010	RWII	0.103	-0.049	0.865	0.028	0.233

Comparisons with closely related species. The new species displays the following characters that are diagnostic of the genus *Quasipaa* (OHLER & DUBOIS, 2006): first finger longer than second; tarsal fold present, external fold along fifth toe extending to the base of the tarsus of this toe; spines on chest of breeding male as a single group, not separated in two lateral patches. Within this genus, the aspect of the dorsal warts in this species agrees with the informal group "*Quasipaa* sensu stricto", as defined above. We provide multivariate analysis and short pairwise comparisons with the four other species currently recognized in this group.

Principal component analysis including size-corrected measurements of *Quasipaa courtoisi*, *Q. exilispinosa*, *Q. jiulongensis*, *Q. spinosa* and *Q. acanthophora* results in 5 principal components with a loading higher than 1 (tab. 3, fig. 2). They provide a rather good summary of the data, accounting for 76.4 % of the total variance (tab. 3). The first principal component shows a high loading for variables of limbs (HAL, TFL, TL, FOL, FTL, ITL), the second principal component mainly describes head shape, having highest loadings from measurements concerning head width (HW) and head length (HL, MN, MBE, MFE); the third component is dominated by variables describing webbing (WTF, WFF, WI, WII); the fourth component shows high loadings for forelimb length (FLL) and internarial distance (IN), and the fifth for distance of nostril to eye (EN) and length of inner metatarsal tubercle (IMT).

Source : MNHN, Paris

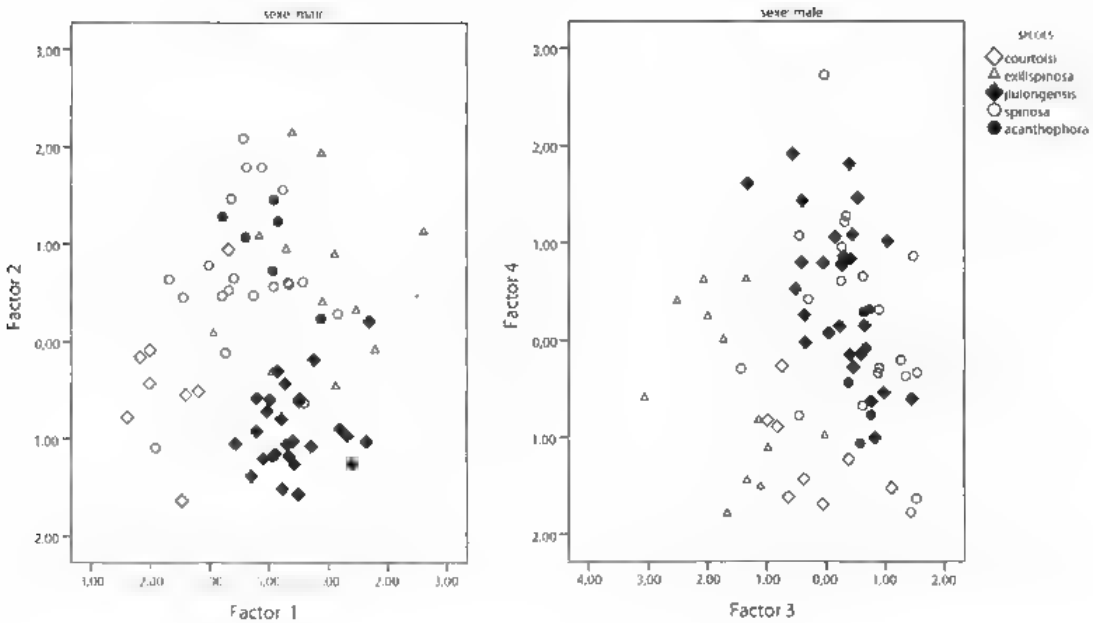

Fig. 2. Results of multivariate morphometric analysis of adult males of *Quasipaa courtoisi*, *Q. exilispinosa*, *Q. julongensis*, *Q. spinosa* and *Q. acanthophora*. Left: plot of principal component factor 1 against factor 2, right: plot of principal component factor 3 against factor 4

ANOVA analysis shows that all these five principal components provide significant discrimination between the five species (tab. 4). Posthoc test shows pairwise significant differences for some of these principal components for all groups studied. PC1 allows significant discrimination of *Q. courtoisi* from all other species and also to discriminate *Q. spinosa* from *Q. exilispinosa* and *Q. julongensis*. PC2 distinguishes *Q. julongensis* from *Q. exilispinosa*, *Q. spinosa* and *Q. acanthophora*, *Q. courtoisi* from *Q. spinosa* and *Q. acanthophora*, and *Q. spinosa* from *Q. julongensis*. PC3 separates *Q. exilispinosa* from all other taxa studied. PC4 shows significant differences between *Q. courtoisi* and *Q. julongensis* and *Q. spinosa*, and between *Q. exilispinosa* and *Q. julongensis*. Thus all species can be discriminated from each other by principal component analysis using morphometric characters, except for the pair composed of *Q. spinosa* and *Q. acanthophora*

The results given above confirm the morphological distinction between *Quasipaa courtoisi* and the other species of *Quasipaa* briefly mentioned, but not documented, by Ohler & Dubois (2006). PC1 allows discriminating *Q. courtoisi* from the other species of this group by lower values of the ratios to SVL of measurements which concern mainly the hands (HAL, TFL), tibia (TL) and feet (FOL, FTL, ITL). PC2 distinguishes this species from *Q. julongensis*, *Q. spinosa* and *Q. acanthophora* by ratios to SVL of measurements which concern the head: width (HW) and length (HL, MN, MFE, MBE) are smaller in *Q. courtoisi* than in *Q. spinosa* and *Q. acanthophora*. But *Q. julongensis* has larger values for HW and MBE than *Q. courtoisi*. PC3 allows to distinguish *Q. courtoisi* from *Q. exilispinosa* by ratios concerning the webbing (WTF, WFF, WI, WII) which are larger in *Q. courtoisi* than in *Q. exilispinosa*

Source : MNHN, Paris

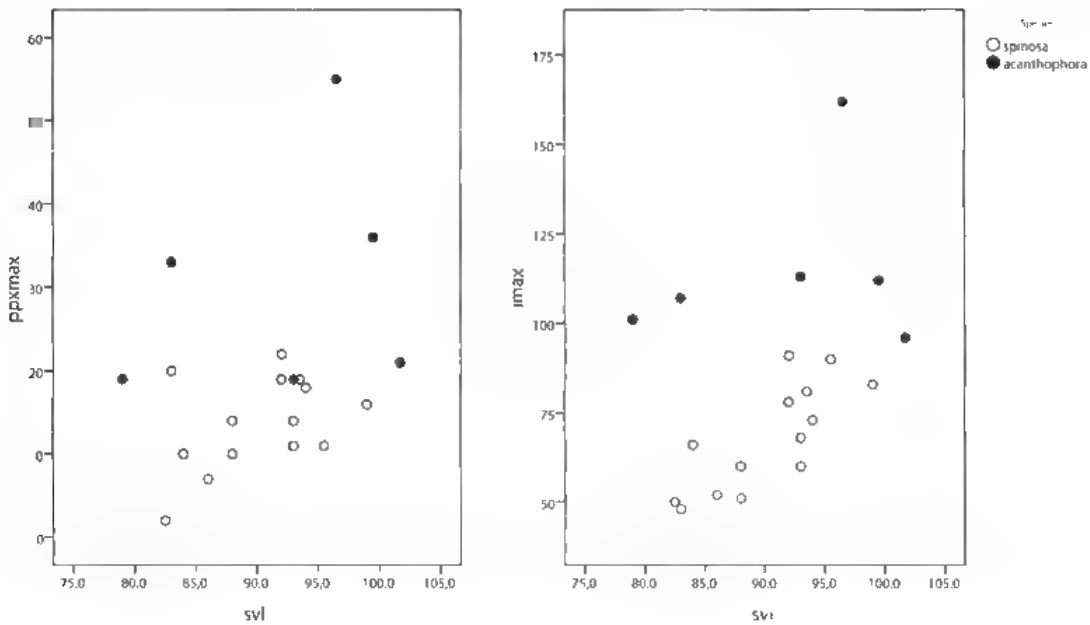

Fig. 3. Maximum numbers of nuptial spines present on prepollex (ppxmax) and finger I (imax), relative to snout-vent length (SVL) in adult breeding males of *Quasipaa spinosa* and *Q. acanthophora*. The value used for each specimen is the maximum number of spines displayed in each frog either on the right or on the left hand.

PC1 distinguishes the new species from *Q. courtoisi* by larger ratios of SVL of measurements concerning the hand (HAL, TFL), tibia (TL) and feet (FOL, FTL, ITL). PC2 allows distinction of these two species by ratios of SVL of measurements concerning the head (HW, HL, MN, MFE, MBE) which are larger for *Q. acanthophora* than for *Q. courtoisi*. PC3 discriminates the new species from *Q. exilispinosa* by ratios of measurements which concern the webbing (WTF, WFF, WI, WII), which is larger in *Q. acanthophora* than in *Q. exilispinosa*.

The new species must be considered a sibling species of *Quasipaa spinosa* (David, 1875) as it does not differ in any of the morphometrical measurements or ratios. Nevertheless this may be due to the heterogeneity of the sample used in this study and considered to be *Q. spinosa*. This sample includes specimens from various regions of China (see app. 1) that are morphologically variable and which most probably consist of several species. Here we recognize the Vietnamese population as a distinct species as these specimens can be distinguished by sexual characters. In many Paini species, adult males show large black spines on various parts of the forelimbs, chest and sometimes venter. Although within a species the number of spines varies according to age and reproductive stage, in several cases very similar species can be distinguished by the number of spines present in some locations (DUBOIS, 1976, DUBOIS & MATSUI, 1983). Figure 3 shows the numbers of nuptial spines on the prepollex and finger I for specimens of *Q. acanthophora* and *Q. spinosa* of similar body sizes. These numbers are significantly different and the numbers of spines on finger I does not even overlap between the two groups: 14 males of *Q. spinosa* have 48-91 spines, whereas 6 males of *Q. acanthophora* have 96-162 spines. (tab. 1)

Source : MNHN, Paris

Beside these differences in male nuptial spines, *Q. acanthophora* differs from *Q. spinosa* in the aspect of warts on back, which are fine and elongate, whereas they are rounded in *Q. spinosa*. The dorsal warts of *Q. spinosa* bear dark, keratinized spinules. These spinules are absent or small and not keratinized in *Q. acanthophora*. Both species exhibit keratinized spines on the dorsal surface of shanks.

Q. acanthophora can be distinguished from *Q. exilispinosa* by adult size, the latter being much smaller. In the sample of the latter species that we measured (see app. 1), SVL of 13 ♂ ranges from 40.0 to 69.0 (mean 55.9 ± 8.40) and that of 11 ♀ ranges from 48.5 to 64.9 (mean 55.6 ± 4.66). Among our *Q. acanthophora* sample, SVL of 6 ♂ ranges from 79.0 to 101.7 (mean 92.1 ± 9.18) and that of our single ♀ is 81.0 mm. If we consider that all the 14 specimens reported by BOURRET (1937) were indeed members of this species (which is quite likely, as all samples of Bourret's amphibian collection in the Paris Museum prove to be monospecific, even if they now bear a different nomen, which suggests that this excellent naturalist had a good "feeling" for species identification), then the extreme values in the Vietnamese species become 89-123 in ♂ and 84-104 in ♀, which shows no overlap with *Q. exilispinosa*. A single ♂ specimen of our sample from Vietnam (BMNH 1903.7.2.26, SVL 61.3 mm) is included in the range of adult males of *Q. exilispinosa*, but, although it shows some spines on prepollex and fingers I and II, it is not yet fully adult, as shown by absence of spines on finger III, so we did not include it in our calculations of tab. 1. Beside size, these two species are also distinguished by webbing, which is less extended in *Q. exilispinosa*: significant differences between them exist for all four webbing measurements used in this study. *Q. exilispinosa* can also be distinguished by its much lower number of nuptial spines on fingers and breast.

The new species can be distinguished from *Q. jiulongensis* by the shape of the head, which is distinctly longer and larger in *Q. acanthophora*. Males of *Q. jiulongensis* also have significantly smaller numbers of spines on prepollex and fingers I and II.

Finally, the new species differs from *Q. courtoisi* in head shape. The head is distinctly longer in *Q. acanthophora*, which shows more distant nares and eyes. The tibia, foot, toes, hand and fingers are longer in *Q. acanthophora*, and the webbing between toes III and IV is less developed in *Q. courtoisi*.

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Source : MNHN, Paris

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Source : MNHN, Paris

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APPENDIX 1

LIST OF SPECIMENS EXAMINED AND MEASURED

Beside the hypodigm of the new species described above, we examined and measured 133 specimens of the four other species here referred to the "*Quasipaa* sensu stricto" group. They are currently or were formerly kept in the following collections: American Museum of Natural History, New York, USA (AMNH); Natural History Museum, London, United Kingdom (BMNH); Chengdu Institute of Biology, Chengdu, China (CIB), Field Museum of Natural History, Chicago, USA (FMNH), Laboratoire de Zoologie de l'Université de Hanoi, Vietnam (LZUH), Museum of Comparative Zoology, Harvard, USA (MCZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN), Zoologisches Museum und Forschungsinstitut Alexander Koenig, Bonn, Germany (ZFMK).

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Quasipaa exilispinosa (Liu & Hu, 1975). – CHINA. (A) *Fujian Province*: (1) Chungan Xian: AMNH 29575-29576, BMNH 1956.1.9.78, 3 ♂, AMNH 28892, 1 ♀, (2) Daiyun Shan: CIB 920037, 1 ♂, CIB 920038, 1 ♀, (3) Kuatin: ZFMK 9723, 1 ♂; ZFMK 9726, 1 ♀. (B) *Hong Kong*: The Peak: BMNH 1956.1.9.79-81, BMNH 1974.2122-2124, MNHN 1988.7892, MNHN 1994.4504, 9 ♂, BMNH 1956.1.9.82, BMNH 1974.2126-2128, MCZ 9423-9424, MNHN 1988.7891, MNHN 1988.7893, 8 ♀.

Quasipaa jiulongensis (Huang & Liu, 1985). – CHINA. *Fujian Province*: (1) Chungan Xian: AMNH 28894-28895, AMNH 28907, AMNH 28909, AMNH 28913, AMNH 28920, AMNH 28922-28926, AMNH 29655-29656, AMNH 29659, AMNH 29661-29662, AMNH 29668, AMNH 29675, AMNH 29677, AMNH 29679-29681, AMNH 29684, AMNH 29745-29748, 27 ♂; AMNH 28908, AMNH 28910-28912, AMNH 28914-28916, AMNH 29485, AMNH 29660, AMNH 29663-29665, AMNH 29669-29671, AMNH 29673-29674, AMNH 29676, AMNH 29678, AMNH 29749-29750, CIB 641.1962, 22 ♀; (2) Wuyi Shan: CIB 920047, 1 ♀.

Quasipaa spinosa (David, 1875). – CHINA. (A) *Fujian Province*: (1) no locality: AMNH 30824, 1 ♂, (2) Amoy: AMNH 44396, 1 ♀, (3) Chungan Xian: AMNH 05410, AMNH 05412, AMNH 28896, AMNH 29198-29199, AMNH 29480-29481, AMNH 29657, AMNH 29667, AMNH 29672, 10 ♂, AMNH 28906, AMNH 29479, AMNH 29482, AMNH 29658, 4 ♀, (4) Futsing Xian: AMNH 05414-05415, 2 ♀, (5) Kuatin: BMNH 1899.4.24.68, ZFMK 9712, ZFMK 9728, 3 ♂, ZFMK 9724, 1 ♀, (6) Pingho: BMNH 1907.10.30.3, 1 ♀, (7) Yenping: AMNH 18457, AMNH 28173-28174, AMNH 28177, 4 ♂, AMNH 08082, AMNH 18450, AMNH 18453-18454, AMNH 28172, AMNH 28175-28176, 7 ♀. (B) *Guangdong*

Source : MNHN, Paris

Province (1) no locality BMNH 1926 10 27 1, AMNH 24314, 2 ♂, AMNH 24315, BMNH 1926 10 27 2, 2 ♀, (2) Lo Fau MCZ 11756, 1 ♂, MCZ 11757, 1 ♀. (C) *Hunan Province*: Yizhang: CIB 75 I.006, CIB 75.I 011, 2 ♂ (D) *Jiangxi Province*: Pinghsiang AMNH 00669, 1 ♂, ZFMK 9749, 1 ♀ (E) *Zhejiang Province*: Ningpo: BMNH 1854.2 10 39, 1 ♀.

APPENDIX 2

LIST AND DESCRIPTION OF MEASUREMENTS TAKEN ON SPECIMENS STUDIED

Body. – SVL, snout vent length

Head. – EL, eye length; EN, distance from anterior corner of eye to nostril; HL, head length (from posterior corner of mandible to tip of snout), HW, head width, at the angle of jaws; IBE, distance between posterior corners of eyes, IFE, distance between anterior corner of eyes, IN, internarial distance, IUE, minimum distance between upper eyelids; MBE, distance from posterior corner of mandible to posterior corner of eye, MFE, distance from posterior corner of mandible to anterior corner of eye; MN, distance from posterior corner of mandible to nostril; NS, distance from nostril to tip of snout, SL, distance from anterior corner of eye to tip of snout, TYD, maximum tympanum diameter; TYE, distance between tympanum and posterior corner of eye; UEW, maximum width of upper eyelid

Forelimb FLL, forelimb length (from elbow to base of outer palmar tubercle), HAL, hand length (from base of outer palmar tubercle to tip of third finger); TFL, third finger length (from base of first subarticular tubercle)

Hindlimb FL, femur length (from vent to knee); FOL, foot length (from base of inner metatarsal tubercle to tip of fourth toe); FTL, fourth toe length (from base of first subarticular tubercle to tip of fourth toe), IMT, length of inner metatarsal tubercle, ITL, inner toe length, TFOL, length of tarsus and foot (from base of tarsus to tip of fourth toe), TL, tibia length, TW, maximum leg width.

Webbing. FFTF, distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe, toes being spread, MTTF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between third and fourth toe, toes being spread, MTFF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between fourth and fifth toe, toes being spread, TFTF, distance from maximum incurvation of web between third and fourth toe to tip of fourth toe, toes being spread.

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Alytes, 2009, **27** (2): 62-66. *Book review*

Asexual and metasexual vertebrates

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John C Avise, 2008 ***Clonality. The genetics, ecology, and evolution of sexual abstinence in vertebrate animals.*** New York, Oxford University Press: i-xi + 1-237. ISBN 978-0-19-536967-0

The focus recently attracted on "clones" by the sheep "Dolly" arose interest in the media for clonal reproduction, a phenomenon that had long been known by biologists. First discovered by the Swiss Charles Bonnet in 1740 in plant lice (Rostand, 1966), the reproduction of virgin females was called *parthenogenesis* by Owen (1849) In the 19th and 20th century, other unusual modes of reproduction were described under the terms of *gynogenesis*, *androgenesis*, *hybridogenesis*, etc Most of these phenomena were first obtained artificially by embryologists in experimental conditions, often in amphibians, before being discovered in nature. Initially thought to be very rare and to occur mostly in "invertebrates", they were found to exist in several groups of vertebrates (fishes, amphibians and reptiles) This book proposes a review of some of these phenomena, called *clonality* by John C. Avise.

An original approach of this book is to consider clonality not only at the organismal, but also at the cellular (mitotic cell divisions) and molecular (DNA replication) levels: "*an individual can be viewed as a huge symbiotic colony of asexually derived clonemate cells*" (p. 13) This approach allows to realize that clonality is a very general feature of all living organisms and explains many of their properties.

At the organismal level, clonality is presented as the "*polar opposite*" of sexuality (p. 30) The evolutionary advantages of both systems are analysed and compared from a theoretical point of view Nevertheless, the fact that both systems do exist in nature shows that none of them is completely superior to the other: according to the conditions, both systems can be efficient.

The book then proceeds to an overview of the characteristics of various unusual reproductive modes, starting with parthenogenesis, gynogenesis, "hybridogenesis" and related systems, then exploring other curiosities like polyembryony, hermaphroditic self-fertilization or human-sponsored clonality All these strange phenomena are briefly described in a very clear language and pedagogic style. This lively text is not only descriptive but also offers many interesting reflections on the evolutionary meaning of the phenomena observed, often with original ideas, as can be expected from a brilliant theoretician of evolution as John C Avise Reading this book is both a pleasure and a very stimulating exercise, as it provokes thought and sometimes suggests views alternative to those of the author.

A real problem with this book, which is not particular to it but has long been a common feature of many "reviews" published by English-speaking authors (see e g. in this respect the comments by Mayr, 1978), is its being largely "US-centered", as it displays a virtually complete ignorance of scientific literature in languages other than English This is particularly annoying in a research field like descriptive and experimental embryology and related ones, where many of the publications, especially in the 19th and early 20th centuries, were published in German, French and sometimes other languages. The presentation

Source : MNHN, Paris

both of the historical facts and of the theories in this book is therefore somewhat biased, although review papers and books on these questions exist in French and German. Nice biographical notes are provided about some United States researchers who significantly contributed to our knowledge of clonality in vertebrates, but the same is lacking for European workers. Hopefully, in a revised edition of this book, these lacks will be filled, perhaps through collaborations with European colleagues.

This book ignores a distinction that was introduced almost 20 years ago (DUBOIS, 1991) and that is important when dealing with such particular "reproductive modes". The latter formula is in fact misleading, as it mixes two very different phenomena: the mode of formation of the gametes (*gametogenesis*) and the mode of activation of the ovum to initiate the development of what then becomes the embryo (germinogenesis or better *kinetogenesis*, from the Greek *kineo*, "I move", to avoid a Latin-Greek "hybrid" term). Gametogenesis can be either sexual (with "normal" meiosis involving reductional divisions or *eumeiosis*), metasexual (with modified meiosis or *metameiosis*) or asexual (meiosis being absent and replaced by simple equational divisions or mitoses, i.e., *ameiosis*). Whereas phenomena like parthenogenesis, gynogenesis and androgenesis are modes of kinetogenesis, the "reproductive mode" often called "hybridogenesis" designates in fact a particular mode of gametogenesis. The embryonic development of the animals that show such a mode of gamete formation usually starts through a fully "normal" kinetogenesis, i.e., fertilization or *zygogenesis*. Mixing both phenomena obscures the analysis of these evolutionary situations, and suggests a misleading "parallelism" between parthenogenesis, gynogenesis and androgenesis on one side, and "hybridogenesis" on the other. As for the complex mechanisms recently described in salamanders of the genus *Ambystoma* under the general term of *kleptogenesis* (BOGART et al., 2007), it covers in fact two different phenomena, abnormal gametogenesis and mixed kinetogenesis processes, involving both zygogenesis and gynogenesis.

The term *hybridogenesis*, improperly stated in the book (p. 81) to mean "*the origin of hybrids*", has long been used in botany and zoology to designate the phenomenon of generation of an organism through hybridization between two organisms belonging in different species. A homonymous term was coined by SCHULTZ (1969) to designate the "reproductive mode" of some fishes, in which in fact it points to a particular kind of kinetogenesis. This term therefore entails several kinds of confusion and should be abandoned. In order to have more terminological clarity, DUBOIS (2008*a*) suggested to keep terms ending in *-genesis* form the categories of kinetogenesis, but to use differently formed terms, ending in *-poiesis*, for the categories of gametogenesis, five of which at least can be distinguished (DUBOIS, 2008*a*, 2009*b*). *Elasopoiesis* is the term that applies to the gametogenesis of so-called "hybridogenetic" organisms sensu SCHULTZ (1969), whereas *tychopoiesis* applies to the gametogenesis of so-called "kleptogenetic" organisms (BOGART et al., 2007). Elasopoiesis results in hemiclonal heredity, with one of the parental hemigenomes being transmitted complete and unmodified, or almost so, to all gametes, whereas tychopoiesis is a more complex mechanism resulting in meroclonal heredity, as it produces various kinds of gametes bearing one or several complete hemigenomes of variable origin, either maternal, paternal or both. Adoption of these distinctions would have made clearer some parts of the discussion of Avise's book.

For the same reason of inappropriate terminology, terms like *parthenogen* or *parthenogenetic* (as adjective or substantive), *gynogen* or *gynogenetic*, *androgen* or *androgenetic*, etc., should be avoided. Let us consider the term *hybridogen*. It is defined in the *Glossary* of Avise's book (p. 184) as "*An individual or strain that reproduces by hybridogenesis*". This definition is too broad and unclear. Individuals and strains are two different things. An individual organism can reproduce, but a strain cannot. We need different terms to designate organisms and strains, just like we have the terms *individuals* and *species* to designate organisms and the taxa in which they belong in the case of bisexual eumeiotic panmictic species. The terms *hybridogen* or *hybridogenetic* are in fact particularly ambiguous as they may have *at least five* different meanings: (1) an individual *produced by* a phenomenon of hybridization, i.e., a first generation hybrid (this is the original and traditional meaning of the term, still of widespread use in botany), (2) an individual *produced by* a hybrid (second or subsequent generation), (3) an individual (of initial hybrid origin, but possibly many generations ago) *which produces* gametes by elasopoiesis, (4) an individual *produced by* gametes one of which at least resulted from an elasopoietic gametogenesis, (5) an individual which possesses *both* these latter particularities. In front of such a terminological confusion, it appears urgent to abandon completely this term, as well as the other ones ending in *-gen* mentioned above, and to use a clearly defined and non-ambiguous terminology. In the case of the term *androgen*, an additional confusion is due to its being identical to a well known term designating a male sex hormone.

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In fact, the use of such terms in this book points to an uncertainty in the way such special organisms should be called. The book uses various formulae to designate them, including the terms discussed above but also "*parthenogenetic lineages*", "*unisexuals*", "*biotypes*", etc. It is not always clear what these terms actually mean, if they apply to individuals, taxa or other non-taxonomic units. Apparently, they just designate "kinds" of organisms, but do not refer them to formal *taxonomic units* or *taxa*. This point of view is difficult to support, because it would imply that only some of the organisms in the world belong to taxa, whereas some others are "outside taxonomy". In fact, this point is little tackled in the book, which does not present a clear position regarding the "species problem", except that in the *Glossary* (p. 189) the following definition is given for *species (biological)*: "*Groups of actually or potentially interbreeding individuals that are reproductively isolated from other such groups*". The taxonomic problems posed by the "special organisms" considered in the book are just mentioned in passing by Avise (e.g., p. 62), but not really discussed. Possibly this means that in his mind only bisexual organisms with normal gametogenesis and kinetogenesis, i.e. corresponding to the "Biological Species Concept" or BSC in the traditional sense (Mayr & Ashlock, 1991), can or should be treated taxonomically. But this would not be consistent with the basic requirement that, to be acceptable, taxonomic systems should be devised in such a way as to accommodate all organisms in the world, whatever their characteristics (Dubois, 1991: 70, 2005: 372). A quite different approach from that of Avise (and of most North American authors as well) has been proposed (Dubois & Günther, 1982, Dubois, 1991, 2007, 2008*a-b*, 2009*b*). This is based first on a clear distinction made between species as a *nomenclatural rank* and as a *taxonomic category*.

As a nomenclatural rank, the term *species* applies to a level in the nomenclatural hierarchy corresponding to the basic unit, the "brick", used in all disciplines of biological research (sometimes far away from evolutionary biology and systematics, like biochemistry, physiology, pathology, etc.), and also in all other non-scientific domains where organisms have to be unambiguously designated, such as environmental conservation, commerce, customs, laws, etc. This is the most widespread use of the term species. In this context, all organisms alive must be uniformly referable to a taxonomic unit of species level, designated by a Latin binomen, that may appear in faunistic lists, juridical texts, etc. For this purpose, it is not appropriate to designate some taxa ("biological species") by Latin binominals, and others by letters or combinations of letters (such as *Poecilopsis* Cx or *Ambystoma* LLJA) or compound names (such as *Poecilopsis monacha-lucida*).

As a taxonomic category, the term *species* may designate various kinds of units, according to the biological properties of the organisms at stake. In order to distinguish this acceptation from the nomenclatural one, these units may be known under the general term of *specion* (Dubois, 2007, 2008*b*), and the different kinds of specions may be designated by terms ending in *-on*, like taxon. The "common" situation is that of the "biological species" or *mayron* (Dubois, 2007), a bisexual panmictic unit whose gene pool is protected from those of other similar units by ecological, ethological, mechanic, biochemical, chromosomal, genetic or other barriers. But other kinds of units can be recognized. These include taxa that depend for their reproduction on other taxa which they so to speak "parasitize" sexually a each generation, either through gynogenesis or through genuine fertilization, and for which the term *klepton* was coined (Dubois & Günther, 1982), as well as unisexual female taxa that reproduce through apomictic or automictic parthenogenesis, which can be known under the term of *klonon* (Dubois, 1991). Several other subcategories can be recognized, and probably some have not yet been identified so far in nature. The general term *kyon* has been proposed for all these categories of "strange species" reproducing through clonality (Dubois, 2008*a*, 2009*b*).

In Europe, most authors use the category klepton (derived from the Greek term *kleptos*, "thief", not from the term *kleptomania*, as wrongly stated by Avise, p. 99) for ranid green frogs of the genus *Pelophylax*, but this has not been adopted by most North American authors. The reluctance of the latter to use special taxonomic units for these entities implies in some cases that they do not want to recognize them as taxa. For example, Frost & Hillis (1990) argued that these frogs with special gametogenesis should be referred formally to the species with which they breed at each generation, just like males are members of the same species as the females with which they breed! This mode of reasoning by analogy is wrong, as in bisexual species males and females are inter-dependent, which is not the case in systems like that of European green frogs, where the klepton indeed depends from the associated mayron for its reproduction, whereas the reverse is not true (see Dubois, 2008*a*, 2009*b*). Others apparently think that these special organisms belong in distinct evolutionary units, which they call "biotypes" or "unisexuals",

Source : MNHN, Paris

but must be kept "outside taxonomy" as they are not "biological species" But the a priori idea that all organisms on earth should belong in a single taxonomic category, a "*unified concept of species*" (e g , DE QUEIROZ, 1998), has no theoretical or empirical justification, and only seems to stem from a reductionist scientific attitude For any evolutionary biologist accustomed to the diversity and unpredictability of life, it is no surprise to realize that different kinds of basic evolutionary units do exist in nature, that cannot be unified except artificially Be it as it may, it is clear that a discussion of the taxonomy of clonal, hemiclonal or meroclonal organisms with asexual or metasexual gametogeneses is wanting in Avise's book, as well as a discussion of the different nomenclatural systems proposed for these taxa (see DUBOIS & GUNTHER, 1982, DUBOIS, 1991, 2008*a*, 2009*b*) Hopefully this will appear in a subsequent edition of this exciting book

This book contains many other interesting discussions, some of which occupy only a few lines but stimulate interesting thoughts. They cannot all be surveyed here, but let us just take one example, which opens a reflection on the conflict that exists nowadays between evolutionary biology and taxonomy on one side, as disciplines which aim at a better understanding of biodiversity on this planet, and conservation biology on the other, which sometimes acts as a break against this progress of knowledge (DUBOIS, 2003, 2006*b*, 2009*a,c*; DUBOIS & NEMÉSIO, 2007; NEMÉSIO, 2009): "*( ) the traditional kinds of data initially suggestive of unisexuality ( ) seem to be gathered less often now because museum workers and systematists generally tend to collect fewer vertebrate specimens. This restraint is due to ethical concerns about declining biodiversity, as well as to stricter laws and protective regulations for vertebrate animals*" (p. 51).

Pursing reflection on these questions leads to realize that, in order to be able to protect some of the extraordinary organisms of multispecific origins that occur in some of these systems, like in the genus *Ambystoma* (BOGART et al , 2007, BI et al , 2009), we need to recognize formally special taxa for them, and to provide them with Latin nomina, as this is indispensable for placing them on official lists of protected taxa (DUBOIS, 2006*a*)

A last comment of general value here concerns these multihybrid organisms. Their mitochondrial genome may in some cases originate from a mayron the nuclear genome of which is totally absent in their genotype (BOGART et al , 2009), so that identifying them through "barcode" would result in a completely wrong taxonomic allocation This suggests that great care should be taken in the use of barcode, as long as so little is known about the gametogenesis and kinetogenesis of most living organisms.

Well, these "strange species" still have a lot to tell us and they no doubt reserve a lot of surprises to biology Rigid-minded people will perhaps be disturbed by these findings, but it is certainly more exciting to learn from nature than only from our models and theories...

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Premiers Tétrapodes

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Sebastien STEYER, 2009. – ***La terre avant les Dinosaures***. Illustré par Alain BENETEAU. Paris, Belin: 1-205. ISBN 978-2-7011-4206-7. 25 €.

Voici un livre fort sympathique. Il se détache par son originalité au milieu de la profusion de livres sur les fossiles célèbres ou les animaux spectaculaires, premiers humains ou Dinosaures, baleines, requins et tigres...

Le titre du livre est un peu trompeur, puisqu'il peut laisser penser qu'il traite de tous les animaux qui vivaient sur les continents avant l'apparition des Dinosaures. En fait, il s'agit du premier livre en français consacré aux premiers Tétrapodes, les premiers Amphibiens et les premiers Reptiles. Le livre frappe d'abord par sa riche iconographie. Il comporte de nombreuses photos de fossiles, des schémas explicatifs, quelques photos de sites fossilifères et de fouilles, mais surtout de nombreuses reconstitutions en couleurs de ces animaux dans leur milieu et "saisis" dans une de leurs activités. Ces "scènes" sont pour la plupart d'une saisissante beauté. Les Amphibiens et les Reptiles sont des animaux difficiles à dessiner de telle manière qu'ils paraissent vivants, et depuis les ouvrages magnifiquement illustrés par Z. Burian dans les années 1960 je n'avais pas vu de reconstitutions aussi réussies.

Une autre particularité de ce livre est sa démarche pédagogique appuyée, pour ne pas dire militante, pour présenter aux lecteurs une interprétation darwinienne de l'évolution, débarrassée de toute idéologie téléologique. L'évolution n'a obéi à aucun plan, aucun dessein préétabli, elle ne se dirigeait pas vers un but, les Vertébrés homéothermes et l'homme ne constituent pas son but ultime et sa réussite absolue. Chaque organisme qui a vécu sur cette planète a été, à un moment de l'histoire de cette dernière, une réussite à sa manière, et aucun organisme n'est "supérieur" aux autres. Ces idées sont bien illustrées tout le long de cet ouvrage, notamment à travers la critique qui y est présentée de deux formules célèbres, connues de tous, mais fausses, celle de "sortie des eaux" et celle de "fossile vivant", qui toutes deux renvoient à une notion de "sens de l'évolution".

Ce livre échappe à une tendance forte actuelle de beaucoup d'ouvrages contemporains, celle d'une présentation "consensuelle" d'une seule théorie là où plusieurs théories sont actuellement en compétition au sein de la communauté scientifique. Ce phénomène de désaccord entre spécialistes est très fréquent en science, bien plus que ne l'imagine souvent le "grand public" à qui souvent l'on cache ces débats. A toutes les étapes de l'histoire de la science, et dans tous les domaines de celle-ci, des théories se sont affrontées, et ceci parfois pendant des décennies ou des siècles. Le fait qu'une théorie donnée soit majoritaire, parfois même fortement, à une époque donnée, n'est en rien une garantie de sa "justesse": l'histoire des sciences est jalonnée de "révolutions conceptuelles", à l'occasion desquelles telle conception hier majoritaire a pu devenir minoritaire, ou même complètement et définitivement abandonnée, en un laps de temps parfois très court, en raison de nouvelles découvertes, de nouveaux concepts ou de nouvelles synthèses. En science, seul le long terme permet souvent de trancher définitivement entre deux théories contradictoires contemporaines. Que l'on pense à cet égard quelques grandes "erreurs historiques" de la communauté scientifique dans le passé, dont rien ne permet d'affirmer que la science est aujourd'hui prémunie (DUBOIS, 2009).

Source : MNHN, Paris

Quelques petites erreurs de terminologie, parfois dues à une influence de la littérature anglo-saxonne, devraient être corrigées dans une réédition de l'ouvrage. Par exemple, si en anglais il n'existe qu'un seul terme (*dentition*) pour les deux concepts, en français, le terme de *dentition* désigne le processus de croissance et mise en place des dents, tandis que le terme de *denture* doit être employé pour désigner le nombre et les types de dents et leur disposition dans la bouche. L'emploi du terme Lissamphibiens pour désigner tous les Amphibiens actuels n'est pas non plus justifié (DUBOIS, 2004), puisque ce terme avait été créé par HAECKEL (1866) pour un taxon comportant les seuls Anoures et Urodèles, mais excluant les Gymnophiones, constituant donc un strict synonyme du terme Batraciens de BRONGNIART (1800); le terme correct pour désigner les trois ordres d'Amphibiens actuels est Néobatraciens de SARASIN & SARASIN (1890).

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Un pionnier méconnu du darwinisme en France

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Yves Carton, 2008 – ***Henry de Varigny, darwinien convaincu, médecin, chercheur et journaliste (1855-1934)***. Paris, Hermann: i-vii + 1-116, pl. 1-7. ISBN 978-2-7056-6822-8. 21,50 €.

Contrairement à une idée souvent répandue, la science avance rarement d'un pas régulier et tranquille, dans un consensus parfait, les nouvelles idées, théories et découvertes étant acceptées par tous et dans le monde entier dès lors que les données et les arguments ont été publiés. Ce n'est qu'à longue, parfois très longue, échéance que les théories considérées "iconoclastes" ou "hérétiques" lors de leur publication peuvent devenir consensuelles – souvent avant d'être à leur tour remplacées ultérieurement par d'autres. Certaines "erreurs historiques" de la communauté scientifique dans le passé font aujourd'hui réfléchir et parfois frémir. Ce fut le cas, par exemple, en France, du rejet quasiment unanime par la communauté universitaire de la théorie chromosomique de l'hérédité, alors même que les preuves de cette théorie avaient été publiées de manière irréfutable aux Etats-Unis – pour briser ce tabou, il fallut attendre la publication du livre *Les chromosomes* (Rostand, 1928) par un "amateur" ne faisant pas partie de l'"establishment scientifique".

Il en va de même du rejet tout aussi vif dans notre pays, pendant longtemps et encore aujourd'hui par certains, de la théorie darwinienne de la sélection naturelle, une histoire bien retracée dans le petit livre d'Yves Carton consacré à la vie et l'œuvre de Henry de Varigny. Celui-ci fut le premier véritable "darwinien militant" français. Dès sa découverte de *L'origine des espèces*, ce médecin de formation, anglophone, docteur ès sciences, ayant travaillé au Muséum national d'Histoire naturelle, se consacra à la diffusion des idées de Darwin, aussi bien vis-à-vis de la communauté scientifique que du grand public. Il publia plusieurs ouvrages sur Darwin et le darwinisme, traduisit en français les lettres de Darwin et d'autres ouvrages sur le darwinisme. Préfigurant ceux de Jean Rostand quelques années plus tard, il écrivit de nombreux articles sur ces questions pour des quotidiens à grand tirage, à une époque où la "vulgarisation scientifique" était rare. Sa démarche est d'autant plus remarquable que la communauté scientifique française se montrait très réticente vis-à-vis de la théorie de la sélection naturelle, dont on peut dire sans exagération que la plupart des "grands savants" de l'époque ne la comprirent tout simplement pas. Il n'est pas à l'honneur de la France que l'Académie des Sciences ait discuté pendant huit ans (près de 3000 jours) de l'élection de Darwin comme correspondant étranger, et encore dans sa section de botanique! Les discussions qui précédèrent ce vote furent édifiantes, comme le montrent certaines "perles" ressuscitées dans l'ouvrage de Yves Carton, comme celle-ci: "*Ses longues recherches sur les races de pigeons (...) prouveraient qu'il manque de véritable esprit scientifique*" (p. 42).

Un tel manque de discernement de la part des "leaders" de la science est-il envisageable aujourd'hui? Rien ne permet d'affirmer le contraire. Ce n'est pas ce qu'on entend actuellement sur la science et son "contrôle" par la société qui peut nous rassurer à cet égard. Des termes jusque là absents du discours sur la recherche, comme "excellence" et "évaluation", y sont désormais d'emploi courant. L'"évaluationnite" actuelle a de quoi inquiéter à plusieurs titres (Miller & Milner, 2004, Lawrence,

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2007, MANIGLIER, 2007). Bien qu'il fût sensible à la contribution particulière de certains "hommes de vérité" au progrès scientifique, mon maître Jean Rostand considérait la science comme une entreprise collective, où chacun apporte sa "petite pierre" à un edifice que n'auraient pu construire seuls quelques "genies". Aujourd'hui, il semble parfois qu'il ne s'agisse plus de savoir si les chercheurs contribuent efficacement à cette entreprise collective, mais de les "classer". Les multiples commissions et instances d'"évaluation" et de classement de dossiers et de candidats auxquelles les chercheurs eux-mêmes sont tous amenés, de gre ou de force, à participer, ressemblent à certains égards à des jurys de jeux télévisés, et leurs classements à des palmares sportifs, des hits parades, des prix littéraires ou des pages du *Guinness Book of Records*. Les curricula vitae, rapports et dossiers de candidature sont de plus en plus truffés de superlatifs. Sous peine de déchoir, un chercheur digne de ce nom, de nos jours, est tenu d'etudier ce qui dans son domaine est "le plus gros", "le plus ancien", "le plus rare", "le plus menacé", ou pourquoi pas "le plus jaune". Il est tres instructif à cet égard d'être attentif dans ces dossiers à de telles affirmations selon lesquelles un chercheur ou une equipe est "le premier" ou "la première", "le seul" ou "la seule" à avoir étudie, trouvé, résolu un problème, une question. Celui qui oserait écrire qu'il a simplement contribue modestement à faire avancer la connaissance dans son domaine de recherche signerait son arrêt de mort institutionnel. L'autre face de la médaille de l'évaluation a tout crin est la forte pression en faveur du conformisme. Rien n'est plus risqué dans ce contexte pour un individu que de ne pas ressembler à l'image du chercheur formate dans ses choix de sujets de recherche, ses idees dominantes, sa maniere d'écrire les articles. les redacteurs, "lecteurs", "referees" et "reviewers" sont là pour veiller à ce que pas une tête ne dépasse et que tous les membres de la grande famille des chercheurs partagent les mêmes opinions, pratiques, conclusions..

Classer c'est hierarchiser, humilier et exclure. La culture du classement est une culture du secret et de l'exclusion, qui s'oppose à la culture de communication et de collaboration qui devrait prévaloir au sein de la communaute scientifique. Il n'est pas très difficile de voir ce qui se joue derrière les formules ampoulees sur l'"excellence": ce sont les réductions de postes, de credits et de locaux, les économies budgetaires et la précarisation des métiers de chercheur et d'enseignant-chercheur. La crise économique et sociale de notre societe mondialisée s'accroît d'annee en année, de jour en jour. Dans toutes les instances d'"évaluation" de la recherche qui se sont multipliées, il ne s'agit plus seulement, comme dans les décennies qui ont précédé, d'associer les chercheurs et les enseignants à la "gestion de la pénurie", il faut les associer à la destruction progressive de leur propre communaute professionnelle, pour en faire de plus en plus, comme dans d'autres domaines de notre societe, de dociles employes precaires et jetables comme des kleenex. Ces objectifs sont ceux annoncés clairement par la Communauté Européenne dans sa "Déclaration de Bologne" (SCHULTHEIS et al., 2008). Quant à la pertinence des "choix stratégiques" de la recherche actuelle, elle est également douteuse, quand on constate que ceux-ci aboutissent à privilégier la recherche de la vie dans d'autres planetes ou le séquençage du mammouth à l'inventaire et l'étude des espèces en train de s'eteindre sous nos yeux sur toute la planete (DUBOIS, 2008*a-b*, 2009*a-b*). Non, il ne semble pas que la communauté scientifique soit devenue plus sage, prévoyante et compétente dans ses choix aujourd'hui qu'elle ne l'etait il y a un siècle et demi.

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Alytes, 2009, **27** (2): 72.

Erratum

In pages 44 and 59 of the article quoted below, an unfortunate mistake has resulted in an inversion between two paragraphs giving the entexognoses of two tribes of the family *Pleurodelinae*. The authors are grateful to Jean-Michel Collet for pointing out this error. The correct texts are given below.

Page 44:

Tribus *Molgini* Gray, 1950

Nucleogenus. – *Molge* Merrem, 1820: 166, by original specific monophory.

Entexognosis. – The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Pleurodeles waltl* (Michahelles, 1830).

Page 59:

Tribus *Pleurodelini* Tschudi, 1838

Nucleogenus. – *Pleurodeles* Michahelles, 1830: 195, by implicit etymological designation.

Entexognosis. – The most inclusive holophyletic taxon including the species *Pleurodeles waltl* (Michahelles, 1830) and excluding the species *Triturus cristatus* (Laurenti, 1768).

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Alytes, 2009, **27** (2): 37-72.

Contents

Thierry Lodé
Mating strategies and monogamy in a territorial breeding anuran, *Rana dalmatina*: a result of sexual conflict? 37-48

Alain Dubois & Annemarie Ohler
A new species of the genus *Quasipaa* (Anura, Ranidae, Dicroglossinae) from northern Vietnam 49-61

Book reviews

Alain Dubois
Asexual and metasexual vertebrates 62-66

Alain Dubois
Premiers Tétrapodes 67-68

Alain Dubois
Un pionnier méconnu du darwinisme en France 69-71

Erratum

Alain Dubois & Jean Raffaëlli
A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela) 72

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